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# PROCEEDINGS OF THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

## SERIES A. GENERAL ENTOMOLOGY

VOLUME 11.

1936.

### LARVAE OF *LUCILIA SERICATA* MG., FROM A CASE OF AURAL MYIASIS REPORTED FROM ESSEX (DIPTERA)

By JOHN SMART, Ph.D., F.R.E.S.

(British Museum, Natural History.)

SOME larvae of *Lucilia sericata* were received last summer for identification from Dr. Scott of Stansted, Essex. A clinical report of the case from which they were taken, by Drs. K. F. Platt and J. A. Scott, has appeared in Dec. 1935, *Brit. med. J.*, 1935 (3909) : 1099-1100, but the occurrence is of sufficient importance to entomologists to warrant the exhibition of the larvae to the Society and a brief record of the facts.

Briefly stated the case ran as follows : the patient, an agricultural labourer, attended at a surgery on the 25th July, 1935, complaining of acute pain in, and a bloody discharge from, his left ear. He told the doctor that two days previously a fly had entered the ear, "buzzed about a minute or two" and come out. The next day the ear became painful and after a sleepless night he reported to the doctor for treatment. The doctor examined the ear and found a mass of larvae packed together in the meatal canal. Syringing with dettol (2 drachms to 1 pint water) caused the maggots to move violently, thus breaking up the dense mass in which they were packed and they were then easily removed. The tissues of the ear were congested and swollen but no perforation of the drum was seen. To ward against secondary infection ear drops (spirit and perchloride) were prescribed and in four days' time except for a slight thickening of the tympanum the ear had returned to normal.

Thirty-one larvae were removed from the ear and 5 of these were sent to me and identified as *L. sericata*.

The case is of interest as it appears to be unique. Writing in 1912 (*Rept. Local Govt. Bd. Pub. Health Med.*, 66) Austen had no cases of aural myiasis to report from Great Britain, and a search of the literature subsequent to that date has not revealed any cases. Cases have been reported frequently from America, but the insects concerned are *Cochliomyia* spp. Infestations of *Cochliomyia* result in a great deal more damage than that reported in the above case. Penetration of the drum may occur (1923, Davis, A. L. L., *U.S. Naval Med. Bull.*, 19 : 345 records two typical cases). In the present case it is unfortunately not known whether any pathological condition existed in the ear prior to the oviposition of the female fly or not.



# NOTES BY COMMANDER C. M. DAMMERS ON THE LIFE-HISTORIES OF TWO SPECIES OF AMERICAN HESPERIIDAE (LEPIDOPTERA)

By Professor HALE CARPENTER, F.R.E.S.

COMMANDER DAMMERS has kindly presented to the department of Entomology, Oxford University Museum, two pairs of each of the Hesperiiids, *Megathymus yuccae navajo* Skin., and *M. stephensi* Skin. Since these magnificent "Skippers" were little known until Commander Dammers succeeded in breeding them recently, some account of the life-histories is of interest. An account is given by J. A. Comstock and C. M. Dammers in 1934, *Bull. S. Calif. Acad. Sci.*, 33 : 81-91. In a letter to Sir Edward Poulton, who has kindly allowed me to make use of it, Commander Dammers wrote: "I have had the honour of first working out the life-history of both; previous to this a few collectors had one or two well-rubbed imagos. Now by breeding it is possible to obtain them in fair quantity and perfect condition. In the case of *M. stephensi* it is possible to go out at night, in their restricted locality, at the time of their flight and with a strong lamp see them sitting on the plants and take them straight into the killing bottle. A most novel way of capturing butterflies. *M. yuccae navajo* lives in the root shoots of the 'Joshua tree' and *stephensi* in the leaf of an Agave, the former becomes full grown in September and passes the winter thus, pupating in March and emerging two weeks after: *stephensi* as soon as full grown in September pupates and emerges in October."

Larvae of *M. stephensi* were first found in October 1932 in San Diego County, California. They inhabit chambers excavated in the lower fourth of a fleshy leaf, near the outer side of the plant. An infested leaf shows no sign of damage. The burrow communicates with the exterior by a minute opening on the upper surface, which is enlarged when the larva is ready to pupate. A silk covering is spun to ensure that a smooth doorway shall be furnished for exit. The inner surface of the chamber is lined with a brown fibrous material which is covered with a delicate layer of silk: it is supposed that the lining is a protection against the viscid gum which is exuded for purposes of repairing the damage done by the larva; this lining must be renewed immediately after feeding.

*M. yuccae navajo* lays eggs on the young shoots of the Joshua tree, *Yucca brevifolia* Engelm., which spring from the long cylindrical roots thrown out from the parent tree. The leaves are semi-succulent. Generally, only one egg is laid on one plant, only one larva can be accommodated on a single shoot. The young larva burrows into the base of a leaf and after consuming the heart works into the root, continually enlarging its burrow so that the top of the plant soon dies. An elongated elliptical chamber is then built as an upward extension of the burrow, incorporating the frass on the outer surface. An opening is made through the walls of the chamber for the voiding of excrement, and is afterwards closed with silk. The larva ceases feeding about mid-September, and covers itself and the inner surface of the burrow with a flaky white substance; it passes the winter thus.

# RATE OF LOCOMOTION IN RELATION TO STARVATION IN *LOCUSTA MIGRATORIA MIGRATORIOIDES* (R. & F.) (ORTHOPTERA)

By K. H. L. KEY, M.Sc., Ph.D., D.I.C., F.R.E.S.

In order to determine whether a state of hunger has any effect on speed of locomotion in *Locusta migratoria*, a method was devised for measuring speed of locomotion under constant conditions, and insects were used which had been subjected to starvation for varying periods.

In all such measurements under controlled conditions, some directive stimulus has to be provided in order to ensure, as far as possible, continuous movement in a straight line. The two stimuli most commonly used for that purpose have been light and gravity; *i.e.*, the organism has been allowed to move up a vertical or sloping plane or rod, or towards or away from a source of light. In doing so it has had to traverse a measured distance, and the time it takes to do so is measured by means of a stop-watch.

Przibram, working with a mantid, Dolley with a butterfly, Cole with *Drosophila*, and Miller with blow-fly larvae, all used light as the directive stimulus, while Crozier with slugs and caterpillars used gravity.

Both stimuli were tried with adult locusts, and it was found that under appropriate conditions the light stimulus gave the more uniform reaction. However, locusts appear to be unfavourable material for this type of work, for hesitations were very frequent.

## *Apparatus and procedure.*

The form of apparatus employed is illustrated in figs. 1 and 2. It consists of two gas cylinders *c*, which can be clamped together mouth to mouth by means of a brass clamp *a*. A rubber ring *r* interposed between the cylinders serves as a gasket. Right down the centre of the chamber thus formed runs a horizontal partition of perforated zinc *z*, which is slightly raised in the centre, as shown in fig. 2, and divides the tube into an upper (*u*), and lower (*s*), portion. Two pairs of yellow lines 15 cms. apart (indicated by arrows in fig. 1) were painted transversely on this zinc to form two measured lengths  $l_1$ ,  $l_2$ , one in each gas cylinder. At each of the closed ends of this apparatus was placed a 50-watt gas-filled bulb *b* immersed in water, and with a water heat-screen *h* interposed between the bulb and the apparatus. The bulbs could be separately switched off and on by means of switches within easy reach of the experimenter. A thermometer *t* was kept in the lower part of the partition. The whole apparatus was painted black outside with the exception of a narrow strip immediately above the centre of the zinc partition, which enabled the observer to follow the movements of the insect inside.

To make a speed determination, the insect was placed in the upper section of the apparatus, which was then clamped, and the insect left in the dark for ten minutes to recover from the stimulation incidental to insertion. Then the left-hand bulb was switched on, and the insect by this means drawn to the left end of the apparatus. Then the left-hand bulb was switched off and the right-hand one simultaneously switched on. The insect would then usually turn at once and commence to walk down the tube towards the right-hand light. The function of the slightly raised centre of the zinc partition is to keep the insect in the centre of the path by utilising its geotropism; otherwise it would



try to climb the glass sides whenever it came in contact with them, and the continuity of the record would be interfered with. As the insect crossed the first transverse line a stop-watch, reading to tenths of a second, was started, and when it crossed the second line, the watch was stopped and the reading taken. The start-stop mechanism on the watch employed was separate from the fly-back mechanism, so that a number of consecutive readings could be taken without returning to zero if desired, and this was done when the insect was moving very rapidly from one end of the apparatus to the other with few hesitations. As the insect passed over the second measured distance a second reading was obtained, and when it had reached the right-hand end of the tube, the right light was switched off and the left light on, and a further two readings were obtained on the return journey.

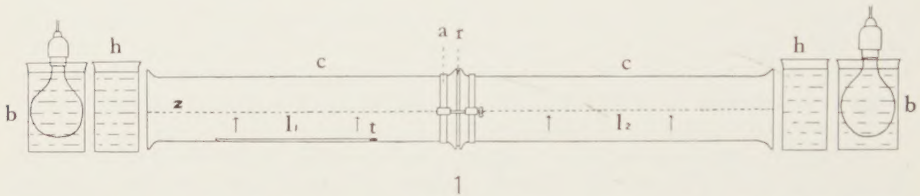


FIG. 1.—Apparatus for determining rate of locomotion. *a*, brass clamp; *b*, electric light bulb immersed in water; *c.c.*, gas cylinders, end to end; *h.h.*, heat screens; *l<sub>1</sub>*, *l<sub>2</sub>*, measured distances of 15 cms. each (between the arrows); *r*, rubber gasket; *t*, thermometer; *z*, zinc partition, dividing the tube horizontally.

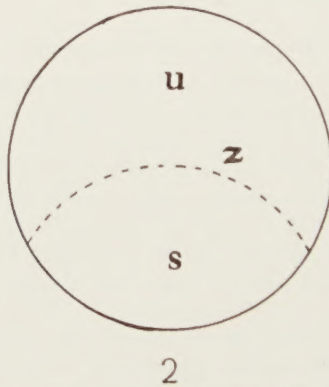


FIG. 2.—Diagrammatic transverse section of the speed apparatus. *s*, lower chamber; *u*, upper chamber; *z*, zinc partition.

In this way readings were obtained in cycles of four: *l<sub>1</sub>*, *l<sub>2</sub>* (left to right); *l<sub>2</sub>*, *l<sub>1</sub>* (right to left). These readings were recorded, and the average times taken to cover each measured strip in each direction computed. Whenever an insect showed any hesitation while moving along the measured strip, the record concerned was rejected. In some cases a high percentage of records had to be rejected on this account. The times taken to traverse the strips in both directions did not show any significant differences, in spite of the fact that the strip nearer the light (*l<sub>2</sub>* when travelling left to right; *l<sub>1</sub>* when travelling right to left) would be at a higher light intensity.

The insects employed for these determinations were kept in a constant temperature room at 27° C. and 35–45% relative humidity, and the deter-

minations were carried out in the same room. The actual temperature inside the apparatus, as measured by the thermometer, averaged 28° C., the greatest difference between the temperatures recorded being 0.7° C.

Four males of nearly the same age and from the same culture were used for the experiment. Two (nos. S1 and S3) were left without food, and the other two (nos. S2 and S4) were fed daily on cut grass. Determinations were made every 12 hours in the order S1, S2, S3, S4. In this way it was sought to discover whether lack of food had any effect upon the rate of locomotion.

TABLE 1. Time (in secs.) taken to cover 15 cms. by starved adult males.

Starvation.	Record.	No. of obs.	Total time.	Av. time.	A.D.	Insect.
12 hrs.	H5	11	37.4	3.40	0.43	S1
12 "	H7	20	67.5	3.38	0.30	S3
24 "	H9	20	78.8	3.94	0.56	S1
24 "	H11	13	58.4	4.49	0.87	S3
36 "	H13	25	58.3	2.33	0.32	S1
36 "	H15	20	65.2	3.26	0.27	S3
48½ "	H17	22	57.1	2.60	0.32	S1
47 "	H19	13	50.5	3.88	0.34	S3
72 "	H21	26	101.7	3.91	0.51	S1
71¼ "	H23	12	51.9	4.33	0.81	S3
98 "	H25	{ 21	86.4	4.11	—	
		{ 36	96.6	2.68	0.21	S1
		239	809.8	3.39	(average)	

TABLE 2. Time (in secs.) to travel 15 cms. taken by normal adult males.

Record No.	No. of obs.	Total time.	Av. time.	A.D.	Insect.
Q	46	155.5	3.38	—	G
H3	22	74.3	3.38	0.30	S3
H1	16	51.6	3.23	0.63	S1
H12	14	62.6	4.48	—	S4
H16	20	64.8	3.24	—	S4
H20	13	48.7	3.75	—	S4
H2	25	85.5	3.42	0.47	S2
H6	8	31.9	3.99	0.39	S2
H10	20	57.9	2.80	0.43	S2
H14	20	64.6	3.23	0.28	S2
H18	21	67.1	3.20	0.36	S2
H27	21	68.3	3.25	0.44	S2
H22	20	64.6	3.23	0.20	S2
	266	897.4	3.37	(average)	

### Results.

Table 1 gives the times recorded for insects S1 and S3 after various periods of starvation, and table 2 the times of the control insects taken at the same time. Each time given is the average of a number of consecutive determinations; 20 was the number aimed at, but sometimes, on account of very irregular progression, this number could not be attained.

The speeds obtained in this way vary from time to time, as much among



the control insects as among those subjected to starvation. If the average time be calculated for all the determinations on all the control insects, and the average time for all the determinations on all the starving insects, the two values obtained are almost identical; they are respectively 3.37 and 3.39 secs. These averages are calculated from the total time and the total number of observations. The number of observations is satisfactorily large.

It may thus be concluded that starvation does not influence speed of movement. No definite relation was found, either, between the number of hesitations necessitating the rejection of a reading, and progressive starvation; the number of such hesitations varied very widely: sometimes the insect moved directly, at others it was constantly stopping for varying intervals, but the number of hesitations did not definitely either increase or decrease with increasing hunger.

If all the observations are combined, an average based on 505 observations may be calculated, which should be characteristic for the conditions of the constant temperature room, and particularly for its temperature of 27° C. This average amounts to 3.38 secs. to cover the 15 cms., which works out at 4.44 cms./sec.

Nymphs of all instars were tried in the speed apparatus, but none of them moved sufficiently directly to enable any records to be taken over the measured distances.

#### Summary.

(1) An apparatus was devised for measuring the speed of locomotion of adult male locusts under the directing influence of a beam of light, and under controlled conditions of temperature.

(2) Insects subjected to periods of starvation up to 98 hours showed no difference in their average speed of movement from normal control insects.

(3) This speed of movement, amounting to 4.44 cms./sec. should be characteristic for the conditions of the experiment, and particularly for the experimental temperature of 27° C.

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### COLLECTED RECORDS RELATING TO INSECT MIGRATION : THIRD SERIES \*

By C. B. WILLIAMS, Sc.D., F.R.E.S.

(Rothamsted Experimental Station, Harpenden.)

IN the course of the last few months a number of observations on insect migration have come to hand which appear to be worthy of putting on record, so that they may be available to all students of the problem. My thanks are due to the senders of the records and also to the authorities of the British Museum (Natural History), as several of the notes came in as a result of the publication by that institution of a booklet on British Immigrant Butterflies and Moths.

\* Series I and II are published in 1928, *Trans. R. ent. Soc. Lond.*, **76** : 79; 1930, *loc. cit.*, **78** : 139.



The following records are given below :—

## Lepidoptera.

### EUROPE.

- (1) *Vanessa cardui* in South England.
- (2-3) *Pieris* sp. in Wales and Ireland.
- (4) *Pieris* sp. in Germany.
- (5) *Vanessa atalanta* in the Irish Channel.

### AFRICA.

- (6-7) *Belenois mesentina* in South Africa.
- (8) *Catopsilia florella* in South Africa.
- (9) *Vanessa cardui* in Nigeria.
- (10-12) *Libythea labdaca* in Nigeria and the Gold Coast.

### AUSTRALIA.

- (13) ?*Belenois java* at Sydney.

### ASIA.

- (14) *Terias hecabe* in Malay.

### AMERICA.

- (15) *Pieris monuste* in Jamaica.
- (16) *Timetes chiron* in Panama.
- (17) *Timetes chiron* and *Catopsilia* spp. in British Honduras.
- (18) *Catopsilia* sp. in Colombia.

## Odonata.

- (19) Dragonflies in Southern France.

### (1) *V. cardui* washed ashore in S. England in 1879.

Mr. S. F. Baddeley has drawn my attention to a letter that he wrote to the *Times* in 1879 (published 23rd August) recording that on the 9th June in that year, when walking along the shore at Boscombe, Bournemouth, he found quantities of *V. cardui* in the sea foam along the water's edge. He wrote : "on breaking the larger bubbles those below were found to contain the same embalmed remains. Later we discovered that many specimens had been drifted to the height of the tide."

Mr. Baddeley now adds that the foam was "simply packed with butterflies" and again "many thousands," and he also states that the discovery followed a violent southerly gale.

The year 1879 witnessed the largest migration of *V. cardui* ever recorded in western Europe, but I had no record of the exact date of their arrival in England which this note now seems to supply.

### (2) *Pieris* (?) *rapae* at Llandudno, North Wales.

Miss B. M. Hitching informs me that on the 15th June, 1930, during the morning (probably between 10 and 11 a.m.) she "walked into a band of white butterflies, small-whites from what I remember, while on the beach at Craig-y-don, Llandudno. The weather was fair with a slight south-east wind. The

butterflies were flying with the wind from the fields out to sea. It would have taken about a couple of minutes to walk across the band; the butterflies being 3-6 feet apart, but varying in distance as they flew. They flew from about 2-3 feet to about 9-10 feet from the ground. I stood among them for about half an hour, but do not know how long they had been passing before I saw them, or continued after I left."

### (3) **White Butterflies in S. Ireland.**

Mr. W. G. P. Evans informs me that on the 15th August, 1913, when he was fishing on Loch Dan in Co. Wicklow, Ireland, in the early morning the fields around were a mass of Cabbage White butterflies (*Pieris* sp.). He watched them for hours and "in the late afternoon they went up in a mass and went off southwards. There must have been thousands of them."

### (4) **White Butterflies in Germany in 1933.**

Mr. Theodor Weilers writes that in August 1933, some time between the 2nd and the 22nd, at Gromitz, Schleswig-Holstein, on the Baltic coast, he observed on several consecutive days a butterfly flight of about 100 to 200 metres broad and of unknown length. The insects were so thick that they made the ground white when they settled on it. The direction of the flight was along the coast from north-east to south-west, and the species was the Cabbage White Butterfly ("Kohlweissling") of from "white to yellowish-white in colour."

### (5) ***Vanessa atalanta* in the Irish Channel.**

Mr. W. G. P. Evans informs me that at the end of July 1920 when he was crossing the Irish Sea from Kingstown to Holyhead, at about twenty miles from the latter port it "simply rained" butterflies. He took one to the Dublin Museum and it was identified as the Red Admiral, *V. atalanta*.

### (6-7) ***Belenois mesentina* at Barberton, S. Africa.**

Mr. E. O. Pearson observed flights of a small white butterfly at Barberton, Natal, South Africa, in December 1931 and in December 1932. They passed over in large numbers towards the north-east for two or three weeks. Mr. Pearson sent me one specimen from the 1931 flight which was a male of *Belenois mesentina*. No specimens of the 1932 flight were captured, but Mr. Pearson considers that it was also the same species. This is made still more likely by the record below.

Mr. J. Marshall sends me particulars of a flight that he and Mr. Pearson observed at Barberton on 18th November, 1935.

The flight started at about 10 a.m. and went on until dusk (6 p.m.). At Mr. Pearson's house the direction was approximately from the north-east to south-west, but at the experimental farm some distance away round a bend in the hills, the flight was due west. There was at the time a slight breeze from the north-east.

Mr. Marshall sent 55 specimens captured by himself and Mr. Pearson, and they included 33 females and 21 males of *Belenois mesentina*, and one *Teracolus omphale* Godt.



(8) *Catopsilia florella* at Barberton, South Africa.

Mr. J. Marshall observed a distinct migration of a large whitish butterfly on the 9th April, 1935. For the previous month only occasional individuals had been seen, but on the 9th April they increased in numbers and in about 45 minutes 63 specimens were seen of which 32 were flying to the east and the others scattered. They were flying against a fresh wind. One specimen was sent, which was *Catopsilia florella*, a regular migrant in south and east Africa.

(9) *Vanessa cardui* in Nigeria.

Mr. F. S. Golding, commenting on the status of *V. cardui* in Nigeria, wrote : " On July 8th, 1935, I saw one very worn *cardui* here [at Ibadan]. I do not remember having before seen this species between May and August." After being away from Ibadan from 13th–26th Sept. 1935 he went into the fields for the first time on the 30th Sept. and saw " four *cardui* all in perfect condition. This is the normal time for the species to appear in the Ibadan area. I have noticed its appearance in September in many previous years."

He added : " I have never seen a migration of this species. They appear very suddenly in September, but there is no evidence that this is the result of migration, except that we have not yet found larvae."

(10–11) *Libythea labdaca* in Nigeria in 1935.

Mr. F. S. Golding wrote that he has seen two migrations of *L. labdaca* at Ibadan, Nigeria, in 1935. The first was on 12th–15th April, when a large migration passed to the south and east. The second was a small migration on the 1st October, also to the south-east.

The first of these is at the usual time of the year for this species, but I have no previous record of a flight in October in Nigeria.

(12) *Libythea labdaca* in the Gold Coast.

Dr. J. M. Winterbottom reports that *L. labdaca* was migrating in considerable numbers at Aburi, Gold Coast, on 23rd March, 1930, from east to west.

(13) White Butterflies at Sydney, Australia.

Mrs. A. G. Irvine informed me that early in 1935, probably in January, millions of white butterflies passed through Sydney, and the beach east of Sydney, flying east out to sea. They were flying quite low down near the ground.

No specimens were captured, but it is almost certain that the species was *Belenois java*, a regular migrant in that part of the world.

(14) *Terias hecabe* in Malay.

Mr. C. N. E. Miller wrote that in June 1933 he saw a flight of thousands of *T. hecabe* going towards the west on the East Coast Road in Pehang, Malay.

(15) *Pieris monuste* in Jamaica in 1886.

Mrs. G. Lister informs me that about noon on the 27th April, 1886, she and her brother, Mr. J. J. Lister, observed a vast migratory flight of white butterflies near Mandeville, Jamaica, all flying in one direction. They drove for miles through a " snow storm " of the butterflies.

Mrs. Lister was kind enough to send me one of the two specimens they had taken and it was *Pieris monuste*, a species known to migrate in Jamaica but more frequently noted in Florida.

(16) *Timetes chiron* in Panama.

Commander J. J. Walker gave me the following record :—

"At Taboga Island, Gulf of Panama, on 3rd June, 1882, when on board H.M.S. *Kingfisher*. There were frequent showers of rain and a large swarming of winged termites alighting on the ship during the forenoon. At 2 p.m. large numbers of *Timetes chiron* suddenly appeared, apparently coming off the island about half a mile distant, flying wildly about the ship and disappearing seaward. A few specimens were caught and also a noctuid moth *Erebias* sp."

(17) *Timetes chiron* and *Catopsilia* spp. in British Honduras.

Mr. R. S. Pelly sent me the following account of a flight of butterflies observed by him on 1st September, 1935, at Middlesex, Stann Creek Valley, British Honduras.

"A large migration from west to east was observed between 8 a.m. and 11.30 a.m. on this date. The brown butterflies [*T. chiron*] were much more numerous than the yellow [*Catopsilia*], outnumbering them about 50 to 1 at a rough estimation. It was a bright day with thunder clouds. Humidity 85 to 90%. Wind light easterly against the flight. The butterflies were making about 8 miles per hour. Altitude of the locality about 450 feet above sea-level."

Mr. Pelly added: "I have observed migrations of the yellow butterflies before, but do not recollect ever observing the brown one."

Eight specimens were sent which included six *Timetes* [*Megalura*] *chiron*, one female *Catopsilia wallucci* Felder and one female *Catopsilia argente*.

(18) *Catopsilia* sp. in Colombia, South America.

Dr. S. C. Harland informed me that in February 1935 he observed a flight of large numbers of yellow butterflies going towards the north for two days across the Magdalena River ten miles from Barranquilla, Colombia.

No specimens were captured, but it is practically certain that the butterflies were a species of *Catopsilia*.

(19) Dragonflies in Southern France.

Miss K. D'O. Twenlow recorded that a large number of red-bodied dragonflies passed over Ciboure, Basses Pyrénées, France, on the 1st and 2nd November, 1935. They were going from a little east of north to a little west of south. They flew high, mostly above the roof (about 35 feet to gable). On the 2nd there was a strong south-west wind and although the dragonflies persisted in their line of flight, many were being whirled about. All flew singly.

Miss Twenlow was unable to catch any but thinks that they were Aeschnidae, from the size and red bodies.

A few were noticed by another observer at St. Jean de Luz about half a mile away.



## THE PROTHORACIC TRACHEAL APPARATUS OF SALTATORIA (ORTHOPTERA) \*

By FRIEDRICH E. ZEUNER, Ph.D.

WHEN studying the phylogenetical relations of the families and subfamilies of Saltatoria I came across an organ the evolution of which, though it took place in the course of millions of years, can still be reconstructed with the aid of Recent forms. It is the lower portion of the tracheal apparatus of the prothorax, which is connected with the tibial auditory organ in members of GRYLLACRIDIDAE, PROPHALANGOPSIDAE, GRYLLIDAE, GRYLLOTALPIDAE, and TETTIGONIIDAE.

A careful study of the prothoracic stigmata and tracheae of Saltatoria was made by V. Graber (1876, *Denkschr. Akad. Wiss. Wien*, 36). Since I was interested in details I dissected specimens of about 35 different species representing almost every family and subfamily of long-horned Saltatoria. My results led me to some conclusions concerning the evolution of the auditory apparatus.

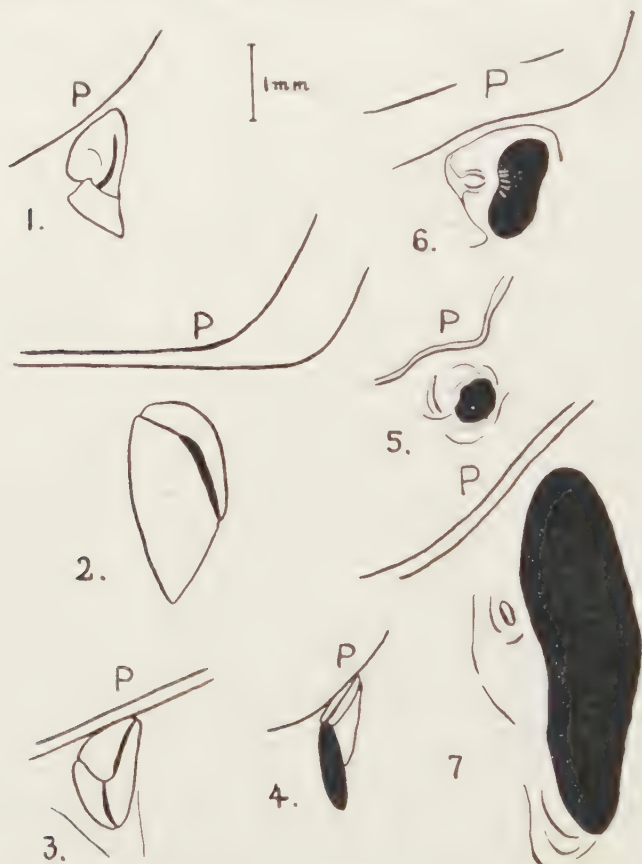
Specimens in alcohol offered little difficulty for dissecting. Dry ones had to be relaxed and could also be studied fairly well, though the truncal tracheae were often destroyed by shrinking. I prefer dissection since it offers an opportunity of studying the exact position of the tracheae in relation to other organs. Moreover, Graber's method of boiling the specimens in potash-lye spoils the finer branches of the tracheae.

The figures given in this paper are schematic so that each of them covers the main characters of several genera. The numerous bends and furcations of the truncal tracheae could not be reproduced in detail. In order to show the truncal tracheae and the femoral apparatus of TETTIGONIIDAE in one figure the truncal stigma had to be moved upwards, though it really lies in front of the femoral stigma. But a comparison of the schematic cross-sections with the figures of the stigmata will enable the reader to correct this inaccuracy. Tracheal branches providing for the organs of the body (muscles, nerves, head, etc.) are shown in black. Only the trachea with its appendages which is connected with the tympanal apparatus in the upper portion of the fore tibia, is hatched ("femoral trachea").

The prothoracic stigma lies near the lower hind margin of the pronotum and above the articulation of the anterior coxa. In GRYLLACRIDIDAE (fig. 1) it is not much distinguished from the other thoracic stigmata. It is small, more or less round, and covered by lids of varying shape. In GRYLLIDAE (fig. 2) and PROPHALANGOPSIDAE (*Cyphoderris*, fig. 3) the prothoracic stigma is more or less oblong and contains the entrances of two tracheal systems which will be described below. It was called "double stigma" by Graber. Lids are present and cover the whole stigma except in *Prophalangopsis* Walker (fig. 4) where the lower (and larger) portion forms an open slit. In TETTIGONIIDAE there are always two separated prothoracic stigmata, one corresponding to the open slit of *Prophalangopsis* ("femoral stigma"), and one corresponding to the upper portion of the double stigma ("truncal stigma"). The truncal stigma lies nearly always in front of the femoral stigma. It is covered by lids and thus resembles closely the primitive stigma of GRYLLACRIDIDAE.

\* This paper is the fourth of a series on the relation between form and function of organs. Previous papers appeared in:—1933, *Palaeont. Z.*, 15: 280; 1933, *Palaeobiologica*, 5: 307; 1934, *Ber. Naturf. Ges. Freiburg*, 34: 21.

The femoral stigma is, as a rule, larger than the truncal one. It is always open, bears no lids but occasionally some hairs protecting the entrance. It is circular in shape in many BRADYTORINAE and their allies, also in PSEUDOPHYLLINAE (fig. 5). In a few genera of these groups it is a little elongated, forming a short oval (fig. 6). In all other subfamilies it is rather oblong, many times larger than the truncal stigma, and often extending vertically over the whole side of the thorax (fig. 7). Being hidden under the pronotum in many PHANEROPTERINAE it is not visible from the outside.

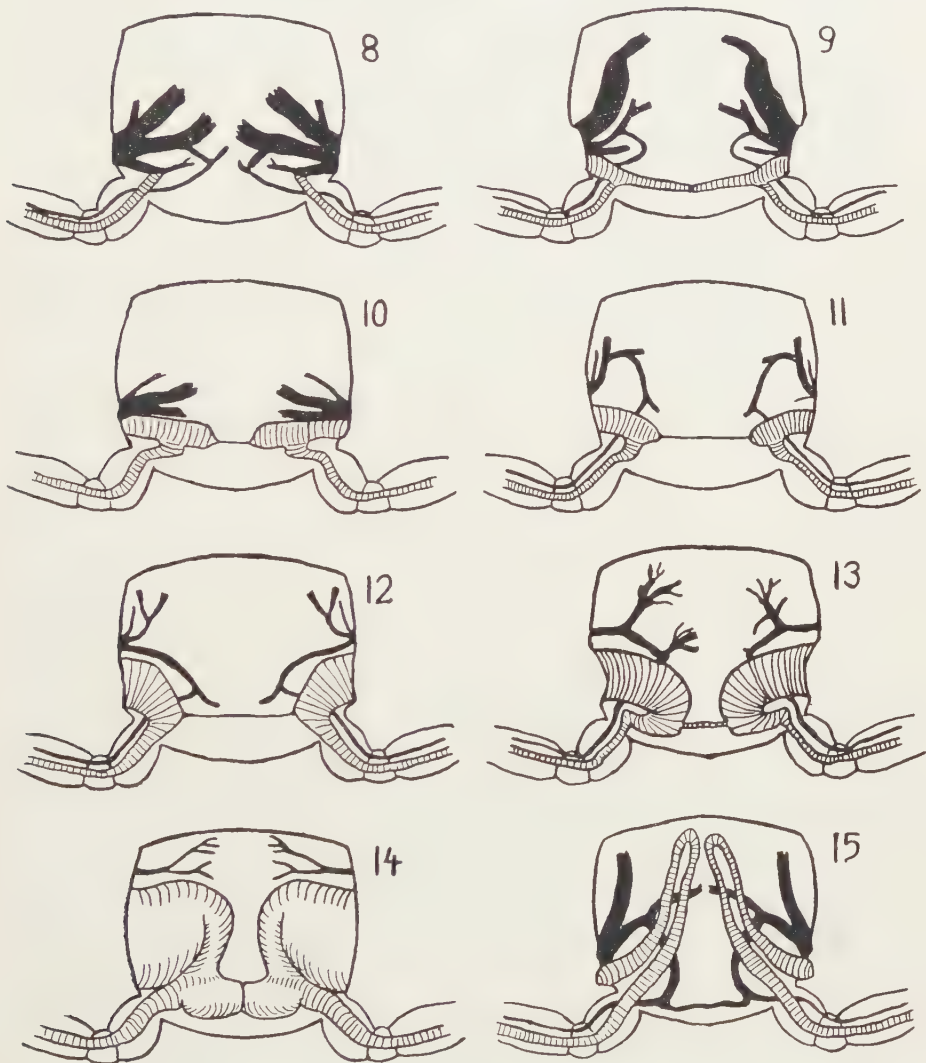


FIGS. 1-7. - Left prothoracic stigmata of Saltatoria. Enlargement the same for all figures. P = margin of the pronotum. 1. simple stigma of *Cratomelus armatus* Bl., 2. double stigma of *Brachytrypes* sp., 3. *Cyphoderris buckelli* Rehn, 4. *Prophalangopsis obscura* Walk., 5. separate stigmata of TETTIGONIDAE, *Cymatomera* sp., 6. *Acanthodis* sp., 7. *Saga ephippigera* F.-W.

It is obvious that these different types of prothoracic stigmata form a perfect "morphological series." As the latter agrees well with the general phylogenetical evolution of the families it may be called an adaptational "step-line" (see Abel, O., *Palaeobiology and Evolution*, to be published shortly by the Cambridge University Press), which though it does not contain actual members of a phylogenetical lineage yet represents the evolutionary stages of an organ by close relatives of the actual members of that lineage.



However, the stigma is merely the entrance to the tracheal tracts which have undergone even greater morphological and functional changes. In GRYLLACRIDIDAE there are several tracheae which leave the stigma and provide thorax, head, and legs, with air. The lowermost main stem gives off a branch entering the fore leg as well as branches for other organs. But that femoral



FIGS. 8-15.—Schematic cross-sections through the hind portion of the prothorax of *Saltatoria*. Explanation see text. 8. *Cratomelus armatus* Bl., 9. *Brachytrypes* sp., 10. *Cyphoderris buckelli* Rehn, 11. *Pycnogaster jugicola* Bol., 12. *Salomona* sp., 13. *Saga ephippigera* F.-W., 14. *Zeuneria* sp., 15. *Cleandrus* cf. *titan* White.

branch is the homologon of the femoral trachea of more specialised forms. It leaves the main stem at an acute angle (fig. 8). There is also a second tracheal branch which enters the fore leg and originates from the *second* main

stem counted from below. This branch is practically always present in GRYLACRIDIDAE, GRYLLIDAE, PROPHALANGOPSIDAE, and TETTIGONIIDAE. It provides the organs of the leg with fresh air and becomes more important in the higher families where the femoral trachea of the lowermost main stem is transformed into a new organ.

In GRYLLIDAE (fig. 9) and PROPHALANGOPSIDAE (fig. 10) the lowermost main stem is profoundly modified. Yet it is evident that the modified portions developed from the primitive Gryllacridid stage. The femoral trachea leaves the lowermost main stem in an acute angle, but it is wider and stronger than in GRYLACRIDIDAE. The main stem itself is widened so as to form an elongated bag ("vesicula femoralis"). The branches providing for other parts of the body have disappeared. Only a very thin trachea continues the bag as far as the middle of the body where it meets, and is fused with, the corresponding trachea of the other side. Thus the vesiculae of either side communicate by this tracheal string ("communicating trachea"). In GRYLLIDAE (*Brachytrypes*) the vesicula gradually decreases in diameter, and the connection is modified as will be described below. As the femoral trachea does not leave the vesicula at its distal end there remains a characteristic "blind end." The latter is found in PROPHALANGOPSIDAE (*Cyphoderris*, fig. 10) and also in TETTIGONIIDAE (*Bradyporus*, *Pycnogaster*, fig. 11, *Amblypterus*, *Orphanina*). As mentioned above these genera have, either double stigmata (Gryllids, Prophalangopsids), or two separate ones (Tettigoniids). In the latter case the truncal tracheae are entirely separated from the femoral tract. There may be several truncal stems of almost equal size, or the second, or second plus third ones are stronger than the others, or the truncal tracheae may even have a common stem originating from the truncal stigma (*Orphanina*). Later it will be seen that there is a tendency to develop a common stem in the more highly specialised genera. The presence of several truncal stems must therefore be considered as a primitive character.

In other TETTIGONIIDAE the vesicula has lost its blind end. It forms, together with the upper portion of the femoral trachea, a horn-shaped, somewhat widened sack. The communicating trachea is usually present. The truncal stems are often separated but sometimes a common stem may be observed. This type of tracheal apparatus is found more or less frequently in all Tettigoniid subfamilies. Among the Bradyporoids I found it only in *Uromemus*, an Ephippigerine (and also in *Acrulocera*, see below), whilst all other genera have vesiculae with blind ends. In the Bradyporoids the horn-shaped vesicula must therefore be considered as a specialised type.

In Pseudophylloids, Tettigonioids, and Conocephaloids, on the other hand, more complicated vesiculae are usually found, but some genera have horn-shaped ones. Thus the latter type appears to be primitive in these groups (fig. 12).

In *Decticus*, *Tettigonia*, and *Saga* (fig. 13), the vesicula has much increased in size as compared with the foregoing forms. The stigma is oval and elongated, and correspondingly, the opening of the vesicula is very large. The vertical diameter of the vesicula decreases gradually within the body, and at the same time the vesicula is strongly curved downwards until it is continued by the femoral trachea. I have called this type of vesicula "trumpet-shaped" to distinguish it from the more primitive horn-shaped one. The communicating trachea seems always to be present.

In certain Conocephaloids, and in many PHANEROPTERINAE, the trumpet-shaped vesicula is found, but it is complicated by an additional expansion



near the origin of the femoral trachea (fig. 14). This expansion is sometimes an almost globular vesicle; sometimes the formations of either side even touch each other in the plane of symmetry. In this case they are pressed against each other and flattened, and a communicating trachea cannot be observed.

I call these additional vesicles the "camerae." They are obviously derived from the original blind ends of primitive vesiculae which have become modified instead of being reduced.

The truncal tracheae of TETTIGONIIDAE with trumpet-shaped vesiculae have always a common stem.

Thus, in close agreement with the shape of the prothoracic stigmata, the tracheal apparatus of the *Saltatoria* in question exhibits a "step-line" of specialisation. It is undeniable that the final type of vesicula with an additional camera is too complicated to serve merely for respiratory purposes. It looks like an "organ" the possible function of which is discussed below. It is, however, advisable first to describe the material on which the present investigation is based.

*Cratomelus armatus* Blanch. (GRYLLACRIDIDAE DEINACRIDINAE).

*Trach.* No vesicula femoralis. At least 4 tracheal stems originating from simple stigma. Lowermost stem sends—apart from other branches into the thorax—one branch into the fore leg. This branch leaves the main stem at an acute angle and is the homologon of the femoral trachea of higher forms. There is also an additional femoral trachea coming from the second main stem. *Stigma* simple, small, with lids. Figs. 1 and 8.

*Gryllacris* sp. (GRYLLACRIDIDAE GRYLLACRINAE).

Two Gryllacrine species were studied. They resemble *Cratomelus* in most respects.

*Gryllacris combusta* Gerst., *Deinacrida* sp., *Rhaphidophora cavicola* Koll., and *Stenopelmatus talpa* Burm. were studied by Graber.

*Brachytrypes spec.* (GRYLLIDAE GRYLLINAE).

*Trach.* Ves. straight, funnel-shaped but slender; fem. trach. leaving at an acute angle. The ends of the funnels of either side touch each other in the middle of the body where they are shut each by a vertical septum with a concentric structure. The two septa touch each other, but the trachea broke here this being a place of minor resistance. A very fine perforation in the centre of the left septum may have been accidental or not. Three truncal main stems present, with an additional fem. trach. from the second one. Third truncal main stem widened in its basal portion. *Stigma* double type, elongated slit with two lateral lids. Graber studied *Gryllus campestris* L. but did not see the septa. *Gryllotalpa vulgaris* L. has also a double stigma from which numerous tracheae originate. Figs. 2 and 9.

*Cyphoderris buckelli* Rehn (PROPHALANGOPSIDAE PROPHALANGOPSINAE).

*Trach.* Lowermost of the 4 main stems transformed into a ves. fem. which is horizontal and of equal width. Blind end long, with communicating trachea. Fem. trach. leaves at an acute angle and is wider at its base. *Stigma*. Fem. st. of the double type, higher than wide, with three lids. Figs. 3 and 10.

*Prophalangopsis obscura* Walk. (PROPHALANGOPSIDAE PROPHALANGOPSINAE).

*Trach.* could not be studied in the unique specimen. *Stigma* considerably elongated,

lower portion open, upper one covered by lids. Double stigma, but transitional to TETTIGONIIDAE. Fig. 4.

*Bradyporus macrogaster* (Lefebvre) (TETTIGONIIDAE BRADYPORINAE).

*Trach.* Ves. fem. shorter than in *Cyphoderris* and somewhat bent down, otherwise similar, with short blind end. Two truncal main stems, first one small, second one by far the largest, with secondary branch as an additional fem. trach. *Stigma.* Two separated stigmata for vesicula and for truncal stems, as in all TETTIGONIIDAE. Truncal st. normal. Femoral st. a straight, narrow slit.

*Uromenus* sp. (TETTIGONIIDAE EPHIPPIGERINAE).

*Trach.* Ves. fem. similar to *Bradyporus*, but blind end reduced, thus reminiscent of *Salomona*. Basis of femoral tr. somewhat wider than in *Deracantha*. No communicating trachea observed. *Stigma.* As in *Bradyporus*.

*Pycnogaster jugicola* Bol. (TETTIGONIIDAE PYCNOGASTRINAE).

*Trach.* Ves. fem. as in *Bradyporus*. Communicating trachea present. Truncal stems three, first and third ones small, second one by far the largest, with a secondary branch as add. fem. tr. *Stigma.* Fem. st. moon-shaped, curved round truncal stigma. Fig. 11.

*Deracantha onos* Pall. (TETTIGONIIDAE DERACANTHINAE).

*Trach.* Similar to *Bradyporus*. No communicating tr. observed. First truncal stem apparently reduced, second one largest, third one smaller. Add. fem. tr. as a secondary branch from second truncal main stem. *Stigma.* Fem. st. smaller than truncal one, circular, and situated below the latter; very primitive condition.

*Enyalipsis* sp. (TETTIGONIIDAE HETRODINAE).

*Trach.* Ves. fem. as in *Bradyporus*. No communicating trachea observed. At least 4 truncal main stems, the first one with a thick branch passing backwards under the vesicula; second one strongest, with secondary branch as add. fem. tr. *Stigma.* Fem. st. short open rectangular slit, in normal position behind the truncal stigma.

*Acridoxena hewaniana* Smith (TETTIGONIIDAE ACRIDOXENINAE).

*Trach.* Ves. fem. small, horn-shaped, blind end reduced. Communicating trachea present? At least 4 truncal main stems, one of them passing under the vesicula. Second and third ones strongest. A branch of the second main stem as an add. fem. tr. *Stigma.* Fem. st. oval but almost round.

*Pterophylla camellifolia* Fabr. (TETTIGONIIDAE PTEROPHYLLINAE).

*Trach.* Ves. fem. similar to *Bradyporus* but blind end almost reduced only a small point being preserved. Communicating trachea present. Four truncal main stems, first one small. Primary branch of the second main stem as add. fem. tr. *Stigma.* Fem. st. short, oval, not larger than truncal one.

*Cymatomera* sp. (TETTIGONIIDAE PSEUDOPHYLLINAE).

*Trach.* Ves. fem. small, horn-shaped, with no blind end, gradually fusing with basis of femoral trachea. At least 4 truncal main stems. *Stigma.* Fem. st. small, circular, elevated. Fig. 5.



*Acanthodis* sp. (TETTIGONIIDAE PSEUDOPHYLLINAE).

*Trach.* Ves. fem. as in *Cymatomera*. Communicating trachea not observed. One truncal main stem, branching early, with secondary add. fem. tr. *Stigma.* Fem. st. short, oval, small. Fig. 6.

*Cleandrus* cf. *titan* White (TETTIGONIIDAE PSEUDOPHYLLINAE).

*Trach.* Ves. fem. a long and narrow tube going up to the back of the pronotum and coming down again, then entering the leg as fem. tr. without modification. No communicating trachea. Two truncal stems, lower one sending an add. fem. tr. into the leg and communicating, through another branch, with the other side. *Stigma.* Similar to *Cymatomera*. Fig. 15.

*Meconema varium* L. (TETTIGONIIDAE MECONEMINAE).

*Trach.* Ves. fem. horn-shaped, small, and curved down. Communicating trachea present. Common truncal stem. *Stigma.* Fem. st. oval, as long as the truncal st., also in *M. meridionale* Costa and *Cyrtaspis scutata* Charp. The fem. st. may be larger in tropical species, or still more reduced (*Nicephora hakgallae* Henry?).

*Macrolyristes corporalis* Karny (TETTIGONIIDAE MECOPODINAE).

*Trach.* Ves. fem. small, horn-shaped, with communicating trachea. At least three truncal stems, with innumerable branches filling the distal portion of the prothorax (in connection with the extraordinary power of stridulation). Add. fem. tr. present. *Stigma.* Comparatively small. Fem. st. oval, truncal st. with large lids.

*Sexava* sp. (TETTIGONIIDAE MECOPODINAE).

*Trach.* Ves. fem. trumpet-shaped as in *Decticus* though comparatively small. Communicating trachea present. Truncal tracheae with a short common stem. Secondary branch as an add. fem. tr. *Stigma.* Fem. st. large, oval, with hairs along the margin.

*Mecopoda elongata* L. (TETTIGONIIDAE MECOPODINAE).

*Trach.* As in *Decticus*. Truncal stem branching earlier. *Stigma* as in *Decticus* and *Tettigonia*.

*Siliquophora grandis* Bl. (TETTIGONIIDAE PHYLLOPHORINAE).

*Trach.* Ves. fem. trumpet-shaped as in *Decticus* but comparatively very small. Communicating tr. present. One truncal main stem which early gives off a fine upper branch which at once becomes very wide and is directed upwards. Add. fem. tr. present. *Stigma* as in *Decticus* but comparatively small.

*Tettigonia viridissima* L. (TETTIGONIIDAE TETTIGONIINAE).

*Trach.* and *Stigma* as in *Decticus*.

*Decticus albifrons* Fabr. (TETTIGONIIDAE DECTICINAE).

*Trach.* Ves. fem. trumpet-shaped, with wide opening, strongly bent downwards; only a small sulcus separates it from the widened basis of the fem. tr. with which it forms a unit. Communicating tr. present. Common truncal main stem, divided but far from the stigma. Secondary branch as an add. fem. tr. *Stigma.* Fem. st. very large, its margin covered by hairs. It is partly hidden under the backward extension of the lateral lobe of the pronotum.

*Saga ephippigera* F.-W. (TETTIGONIIDAE SAGINAE).

*Trach.* As in *Decticus* and *Tettigonia*. Trumpet very large. Three branches of the truncale stem enter the fore leg, one of them being the usual add. fem. tr.; the others are supplementary. *Stigma* without marginal hairs. Figs. 7 and 13.

*Salomona* sp. (TETTIGONIIDAE SALOMONINAE).

*Trach.* Ves. fem. horn-shaped, comparatively small. Similar to *Acanthodis*. Communicating tr. present. Four truncale main stems, first and fourth ones small, second one largest, with branch as an add. fem. tr. *Stigma*. Fem. st. rather large, broad, oval, with hairs. Fig. 12.

*Amblylakis inermis* Redt. (TETTIGONIIDAE SALOMONINAE).

*Trach.* Ves. fem. as in *Bradyporus*, with blind end and communicating trachea. One large truncale stem, and a very small one leaving the main stem near the stigma in an upward direction. *Stigma*. Fem. st. short and oval.

*Agraecia maculata* Redt. (TETTIGONIIDAE SALOMONINAE).

*Trach.* Ves. fem. trumpet with a sharp terminal bend (corresponding with blind end). Short common truncale stem. *Stigma*. Fem. st. large and oval, truncale one in front of the former but rather basally.

*Bucrates* sp. (TETTIGONIIDAE COPIPHORINAE).

*Trach.* Ves. fem. a small trumpet with a short blind end. Truncale tr. destroyed in the specimen examined. *Stigma*. Fem. st. oval, almost concealed under the pronotum.

*Conocephalus turanicus* Sem. (TETTIGONIIDAE CONOCEPHALINAE = XIPHIDIINAE).

*Trach.* Ves. fem. large trumpet with small camera. Short truncale main stem? Fem. st. as in *Decticus*, very large.

*Homorocoryphus* sp. (TETTIGONIIDAE COPIPHORINAE).

*Trach.* Ves. fem. similar to *Zenneria*, but camerae not pressed against each other, and vesiculae directed inside, not forwards. One truncale main stem. *Stigma* similar to *Decticus*.

*Hexacentrus* sp. (TETTIGONIIDAE LISTROSCELINAE).

*Trach.* Ves. as in *Decticus*, other tracheae destroyed in the specimen. *Stigma* as in *Decticus*, very large.

*Tympanophora pellucida* White (TETTIGONIIDAE TYMPANOPHORINAE).

*Trach.* Ves. fem. as in *Homorocoryphus*, truncale tr. destroyed. *Stigma*. Fem. st. oval, short and broad.

*Orphanidia denticauda* Charp. (TETTIGONIIDAE PHANEROPTERINAE).

*Trach.* Ves. fem. directed inside, horn-shaped, but with a blind end. The latter is somewhat globular (camera?). Communicating tr. doubtful. Weak common truncale stem. *Stigma*. Fem. st. comparatively small, oval. Truncale st. in the middle front of fem. one, with large lids.

*Eurycorypha* sp. (TETTIGONIIDAE PHANEROPTERINAE).

*Trach.* Ves. fem. a strongly curved trumpet which is directed forward. Camera very



small but distinct. Communicating tr. not seen. *Stigma*. Entirely hidden under the pronotum as in *Stilpnochlora*. Hind margin of pronotum fitting into the mesothorax. Truncal st. very low, near the base and externally of the fem. one.

*Stilpnochlora* sp. (TETTIGONIIDAE PHANEROPTERINAE).

*Trach.* Ves. a strongly curved trumpet, directed forward the fem. st. being directed backward. Ves. joins the fem. tr. by a sharp bend. Camera absent, but otherwise the arrangement similar to *Zeuneria*. The trumpets do not touch each other because of their forward direction. Truncal tracheae reduced. *Stigma*. Fem. st. large and long, as in *Eurycorypha*.

*Zeuneria* sp. (TETTIGONIIDAE PHANEROPTERINAE).

*Trach.* Ves. fem. as in *Stilpnochlora* but with a large camera. The camerae of either side are pressed against each other in the plane of symmetry, therefore communicating tr. absent. Truncal tr. with common stem. *Stigma* as in *Decticus*. Fig. 14.

The question whether the vesiculae of genera like *Saga* (fig. 13) or *Zeuneria* (fig. 14) have a special function, must be answered in the affirmative. In GRYLLACRIDIDAE, the original femoral trachea and the lowermost tracheal main stem leaving the stigma are distinguished in no way from the other tracheal stems and their branches (fig. 8). It is noteworthy that the second main stem also produces a branch entering the fore leg. This branch probably is preserved in all higher forms and has actually been observed in most of the species studied.

The true femoral trachea which was to undergo so great specialisation, is the one that supports the tibial auditory tympanum from within. It is easy to understand that it is advantageous for the accurate reception of sounds if in this trachea the air does not pulsate as in ordinary ones. Furthermore, as Prof. Rankine kindly pointed out to me,\* the femoral trachea acts as a resonator when air is passing through the main stem so that a sound is produced in the former. Thus there is double reason for improving this tracheal apparatus. Indeed, PROPHALANGOPSIDAE and GRYLLIDAE have acquired a widened basis of the main stem (the "vesicula"), and a widened basis of the femoral trachea (figs. 9, 10). In addition, the lowermost main stem tends to become separated from the others, the stigma becoming "double" with two compartments but still with common lids (figs. 2, 3). In *Prophalangopsis* the lids are already restricted to the truncal portion of the stigma leaving the femoral portion open. The truncal branches of the lowermost main stem are rapidly reduced so that there remains, apart from the femoral trachea itself, only the fine connection of the vesiculae of either side.

The horn-shaped and trumpet-shaped vesiculae of many TETTIGONIIDAE are still better organised. Their entrances are entirely independent of those of the truncal tracheae, they are widely open and not covered by movable lids (figs. 5, 6, 7). Thus the air in the femoral trachea communicates freely with the air outside the body, and the whole system is not affected by air pulsating in the tracheae.

At this stage of evolution the vesiculae proved to act as receivers of sound since the open communication of the vesicula with the air surrounding the

\* I am greatly indebted to Professor A. O. Rankine, of the Imperial College of Science, for the kind interest he took in my investigation, and for some valuable suggestions.

animal allowed sound waves to enter the femoral trachea. This probably was not the original purpose of the tracheal organ. There was an obvious need to modify the shape of the lowermost tracheal main stem and to reduce all trunical branches emanating from it in order to diminish disturbing noises caused in the femoral trachea by pulsating air. Such sounds were to be heard by the nerval organ in the tibia which originally was intended to receive sounds only through the external tympanum of the tibia. But the new arrangement which was free of the disturbing noises, at the same time allowed sound waves to meet the tibial nerval organ from within. According to Prof. Rankine, to whom I suggested the possibility of an interference of the phases of waves meeting the nerval organ through the tympanum, and, on the other hand, through the femoral trachea, half the average wave length of the sounds in question is considerably greater than the length of the femoral tract. Thus, interference is very unlikely and a reinforcement of the sound perceived by the nerval organ is the inevitable result.

Though one has to be careful in applying the laws of reflection to organs which are small as compared with the wave length, there is no doubt that the large trumpets (fig. 13) serve their purpose better than the horn-shaped vesiculae (fig. 12). It would be worth studying the exact purpose of the additional "camera" found in certain *Conocephaloids* and *Phaneropteroids*. Prof. Rankine is inclined to explain it as a resonator which tunes the whole tract for a certain sound (if so, probably the stridulating sound of the species).

Thus, the lowermost main trachea in the prothorax of long horned *Saltatoria* offers a further instance of an imperfect change of function of an organ, just as does the stridulating organ on the elytra of *Saltatoria* (Zeuner, F., 1934, *Nature*, 134: 460). Originally intended to provide certain parts of the body and legs with air, the tracheal tract is transformed into a sound receiving apparatus; but the primary function seems not to be abolished entirely. The femoral trachea is continued into the tarsi and provides the tissues of the leg with air by means of a few very small branches. Furthermore, it is connected with the vesicles in the pulvilli. It is likely that the movements of the latter, and those of the whole leg, are sufficient to ventilate the air in the femoral trachea. At any rate the breathing function of the femoral trachea is much reduced but not quite abolished.

The original sound receiving organ is the external tympana of the fore tibia. The tympana have so far retained their function of vibrating under the impacts of sound waves. This, however, is also the function of the walls of the lower portion of the tibial trachea. It is not impossible that in the course of future evolution the tympanum will disappear as unnecessary.

The nerval organ was originally one of the numerous "scelopiferous" organs of the body. Having acquired a sensibility for sound waves it has maintained its function of perceiving sounds through the tympanum. Later, an additional resonator and sound receiver was developed (the tracheal tract). In this connection it is necessary to recall the composition of the nerval organ of *TETTIGONIDAE* (Graber 1876, and Schwabe, J., 1906, *Zoologica, Stuttgart* 50). It consists of the "subgenual organ" inserted at the walls of the tibia immediately above the tympana. (This is the original nerval organ which is also found in many non-*Saltatorial* insects without any tympana.) The "intermediate organ" connects the subgenual organ with the "crista acustica" which extends downwards and is attached to the (thicker branch of the here twofold) trachea.

This arrangement is found in the *TETTIGONIDAE* with their complicated



vesiculae. In GRYLLIDAE which have more primitive vesiculae, the "crista acustica" is missing and replaced by an apparently simpler kind of tracheal nerval organ. In GRYLLACRIDIDAE which have an undifferentiated tracheal tract without vesiculae, neither a "crista" nor its equivalent has been found (Graber: 133, explanation of fig. 54). It is only logical to conclude from these facts that the "crista acustica" was specially developed in the TETTIGONIIDAE for the reception of sounds through the wall of the femoral trachea.

This is important. The TETTIGONIIDAE have acquired not only a second apparatus for transmitting sounds to the nerval end organ, but a second nerval organ has appeared on the trachea, probably as an extension of the subgenual organ. Thus the TETTIGONIIDAE are provided with "double ears," the tympana with the subgenual organ, and the femoral tracheal tract with the "crista acustica." Should the tympana with the subgenual organ be artificially destroyed—or be reduced in the natural course of phylogenetic evolution—the insects would still be capable of hearing. This looks much like the replacement of one sound-receiving organ by another one of a more effective construction being in progress.

Many details still remain to be studied. Observations on the ontogenetical evolution of the organs in question would be particularly useful. I may mention also that in some cases a connection of the vesicula with the prothoracic ganglion may be seen but so far I have not studied its structure. The main object of the present paper is to provide more evidence for the phylogenetic relations of the families and subfamilies, which will shortly be treated separately. (1936, *Proc. R. ent. Soc. Lond.* (3) 5.)

## LARVA OF THE WHITE ERMINE MOTH SWIMMING ACROSS A STREAM

By Miss C. E. LONGFIELD, F.R.E.S.

THE following entry is from my diary for 1916. I was reminded of the incident, and looked up the entry, on reading about the aquatic Arctiid larvae in our *Proceedings*.

"September, 1916. Watched a last instar or possibly a full fed caterpillar of the White Ermine Moth, *Spilosoma menthastris* Esp., swimming across the stream in the Lower Park. Whether it had accidentally fallen in or had deliberately entered the water, I could not say, as when I first saw it, it was strongly breasting the hummocks and eddies of the swift stream. At this point the stream is about 10 feet across, clear, and running strongly. The caterpillar was swimming with apparent ease, very fast, with head pointed up-stream. It was high in the water, no doubt buoyed up by its thick hairs. It was swept about 2 feet down-stream before reaching the farther side."

The park is at my old home, Castle Mary, Co. Cork, Ireland. It is a grass Deer Park, with rushes and bracken. Two species of Water Mint grow by the stream. The stream is always a swift one, and I remember being so very astonished at the swimming powers of this caterpillar.

*PSEUDACRAEA EURYTUS* (L.) AND ITS MODELS IN THE BUDONGO FOREST, BUNYORO, WESTERN UGANDA (LEPIDOPTERA)

By Professor G. D. HALE CARPENTER, F.R.E.S.

THE highly complex association of forms of the Nymphaline species *Pseudacraea eurytus* (L.) with various species of the Acraeinae genus *Bematistes* (Hemming, 1935: this name replaces *Planema* hitherto incorrectly used for this genus), which they and other Lepidoptera resemble, has been closely studied in several localities in Uganda. Through the kindness of Mr. T. H. E. Jackson, F.R.E.S., I am now enabled to give a complete account of a collection made by him in the Budongo forest, Bunyoro, western Uganda, during September 1934. A large selection from this was presented to the Department of Entomology in the Museum of the University of Oxford by the generous collector, including types of two forms which have been described as new (1935, *Proc. R. ent. Soc. Lond.*, **10**: 22; *ibid.*: 57-9, and pl. 2). Previous investigations having shown that the Budongo forest is an exceptionally interesting locality (1933, *Proc. R. ent. Soc. Lond.*, **8**: 109), I urged Mr. Jackson to obtain a large collection so that the proportions of models and mimics might be compared with those previously recorded in other parts of Uganda (1924, *Trans. R. ent. Soc. Lond.*, **1923**: 469 for references).

The following results emerge from the accurate records kept by Mr. Jackson of all specimens captured.

It appears that, at the time when he collected, *Bematistes schubotzi* Grunb. took the place of *B. tellus eumelis* Jord., which, in my experience, is generally the most abundant of the species of *Bematistes* entering into this association in Uganda. Moreover, the brilliantly white subapical patches on the fore-wings of *schubotzi* females are associated with corresponding modifications of *Acraea althoffi* Dew. and of *Pseudacraea eurytus* (1935, *loc. cit.*). It is most interesting to find in a new locality such corroboration of previous work on the correspondence of forms of *eurytus* to the prevailing species of *Bematistes* in each locality.

The more these minute details of geographical distribution are studied, the more inadequate appears such an explanation of mimicry as is constantly urged by Herr F. Heikertinger of Vienna. He, by reproducing in black and white the patterns of various butterflies, claims to show that there is no need to invoke a mysterious process of mimicry by natural selection: the similarity of pattern between two or more species of butterfly results from the appearance of a very simple pattern in species, which, after all, are members of the same order and might be expected to show similar pattern. This extremely crude argument entirely ignores resemblances between insects of very different orders: it ignores the fact that a similar appearance may be produced in entirely different ways; and, in particular, it takes no notice of the precise correspondence between models and mimics such as I have previously demonstrated in the case of *Pseudacraea eurytus*, and am now about to demonstrate in a new area.

*Combination I.*

Orange bar across fore-wing, white bar across hind-wing; two subdivisions differing slightly in direction and tint of orange bar.

PROC. R. ENT. SOC. LOND. (A) 11. PT. 1-2. (MAR. 1936).



A. Primary model.		Associated rare species.	Acraeine mimic.	Nymphaline mimic.
<i>Bematistes macarista</i>		<i>B. macaria hemileuca</i>	<i>Acraea alciope</i> ♀ f.	<i>Pseudacraea eurytus</i>
E. M. Sharpe, ♂.		Jord., ♂.	<i>aurivillii</i> Stgr.	(L.) ♂ f. <i>hobleyi</i>
2		2	50	Neave.
			Non-mimetic ♂.	4*
			49	
B. Primary model.		Nymphaline mimic.	Elymniine mimic.	
<i>B. poggei nelsoni</i>		<i>Ps. eurytus</i> , ♀ f. <i>poggeoides</i> Neave.	<i>Elymniopsis phegea</i> f.	
Gr. Sm. ♂, ♀.		1	<i>rattrayi</i> E. Sh. ♂, ♀.	
0			2	

No specimens were seen of the following mimics which have been recorded from other localities :—Nymphalinae; *Pseudacraea kunowi hypoxantha* Jord., *Precis ranana* Gr. Sm.; Papilioninae, *Papilio d. dardanus* Brown, ♀ f. *planemoides* Trimen.

The members of this combination, except *A. alciope*, were much less prominent than in previous records from any part of Uganda. The abundance of *alciope aurivillii* is remarkable; it must be remembered, however, that it is synaposematic and not pseudaposematic. The other chief female form of this species characteristic of west Africa, of which occasional specimens occur at Entebbe, resembles the brown western species of *Bematistes* of which none occurred in Budongo forest. Seventeen of these brown *alciope* females were taken by Mr. Jackson.

The sub-group B of the combination is even less well represented. No specimens of the model were seen, and none of the Papilionine mimic in its fully developed form, although Mr. Jackson recorded one specimen transitional to *planemoides*. A single Nymphaline mimic, and two Elymniine mimics are recorded.

### Combination II.

Black and white.

Primary models.		Acraeine mimics.	Nymphaline mimic.	Elymniine mimic.
<i>B. macarista</i> , ♀.	4	<i>A. jodutta</i> ♀ f.	<i>Ps. eurytus</i> ♀ f.	<i>Elymniopsis</i>
<i>B. alcinoë camerunica</i> Jord., ♀.	1	<i>jodutta</i> F.	<i>tirikensis</i>	<i>phegea</i> f.
<i>B. macaria hemileuca</i> , ♀.	2	<i>A. althoffi</i> ♀ f.	Neave. 10	<i>bammakoo</i>
<i>B. a. camerunica</i> , ♂,		<i>althoffi</i> Dew. 30		Westw., ♂, ♀. 1
not entering this association.	1	<i>A. althoffi</i> , ♂, not entering this association. "Very common."		

This well known combination again shows scarcity of models: the lack of *B. alcinoë* is especially noteworthy as it is usually abundant in central Uganda and in west Africa. The specimens of *tirikensis* which Mr. Jackson kindly sent me are variable and at one end of the series might more justly be named *simulator* Butler, as the posterior half of the angulated white band across the fore-wing is lacking, so that there is only an oblique subapical bar. *Bematistes aganice montana* Butler, so common in the eastern parts of Uganda and reaching to Entebbe, has not yet extended to the Budongo forest (1924, *Trans. ent. Soc. Lond.*, 1923 : 483). *A. jodutta* and *A. althoffi* are both abundant, and illustrate the complications of these mimetic relationships. While both have black and white female forms resembling *Bematistes*, *althoffi* also has a yellow form *ochreata* Eltr., resembling the male *jodutta*, 23 were taken and 51 ♂ *jodutta*.

\* The h.w. bar is purely white in 3, suffused with yellow externally in 1.

These two may be termed *Combination III* : the pattern is as in the next combination but the colour yellow instead of brownish-orange.

#### *Combination IV.*

Black and brownish-orange. This combination, usually the commonest in Uganda, centres round the abundant *Bematistes tellus eumelis* Jordan, and is closely associated in west Africa with the ♂ of *B. epaea epaea* (L.). It must be noted that the unusually abundant *B. schubotzi*, which through its female is the basis of the next combination, in Budongo adds its males to the male and female of *B. tellus* which elsewhere form the only primary models for group IV.

Primary model.		Acraeine mimics.		Nymphaline mimic.
<i>Bematistes tellus eumelis</i> Jordan,	<i>B. schubotzi</i> Grunb.	<i>Acraea jodutta</i> ♀ f. <i>dorotheae</i> Eltr.	<i>A. althoffi</i> ♀ f. <i>telloides</i> Eltr.	<i>Pseudacraea eurytus terra</i> Neave, ♂, ♀.
♂, ♀. 3	♂. 3	14	13*	2†

One of the *jodutta dorotheae* is transitional to the previous form *j. jodutta*. There are also 3 specimens reported by Mr. Jackson which appear to combine the features of more than one form. One of the *althoffi telloides* was taken in copula : the specimens are variable in the depth of the brownish-orange colour.

No specimens of the Papilionine member of this group were seen (*P. d. dardanus* f. *niobe* Auriv.).

#### *Combination V.*

Differing from the last by the pure white subapical bar and, sometimes, the white hind marginal area, this interesting addition to the various patterns already known in these mimetic associations is the central feature of this paper.

Primary model.	Acraeine mimics.		Nymphaline mimic.
<i>Bematistes schubotzi</i> ♀.	<i>Acraea jodutta</i> ♀ f. <i>integra</i> Schultze & Auriv.	<i>A. althoffi</i> ♀ f. <i>budongensis</i> Carptr.	<i>Pseudacraea eurytus</i> ♀ f. <i>schubotzoides</i> Carptr.
14	2	2	7

This combination was described for the first time by myself in 1935, *Proc. R. ent. Soc. Lond.*, 10 : 22-23; 57-59 and pl. 2. The male *schubotzi* is very like *tellus*, but the orange colour is richer. Occasional specimens of *tellus* show the pale subapical bar on the fore wing to be tending towards white as in the male and one of the female specimens listed above : it would be interesting to study a large number of *tellus* from Budongo and ascertain if a considerable proportion show this approach to the characteristic appearance of *schubotzi* female. The inner marginal patch of the fore-wing in the female *schubotzi* may be of purest white (1), or suffused with orange (5), or orange like the rest of the wing (4). One specimen which I have not seen is reported by Mr. Jackson to have all the pale areas of the fore-wing of a "pale yellow" tint. It is most interesting to find that the brilliantly white subapical patch of the female *schubotzi* occurs in the usual associates of *Bematistes*, *Pseudacraea eurytus* and two species of *Acraea*.

In the case of *Pseudacraea eurytus* I have described (1914) forms on the Sese Isles in which the subapical band is whitish, owing to admixture of the form *tirikensis*, but in none of these intermediate specimens does the size or whiteness of the band equal the brilliantly white band of *schubotzoides*. More-

\* Only one is of the typical dark orange-brown, the rest are transitional to *ochreata* Eltr.

† One has inner marginal patch on f.w. much paler and is transitional.



over, in these intermediate specimens there is much more of the reddish triangle at the base of the hind-wing on the underside, derived from *tirikensis*, than in *schubotzoides* which has no need of this aposeme since it is absent from the model, *schubotzi*. The presence of *schubotzi* type of coloration in a form of *Acraea jodutta* may be commented on as an example of how closely two types of conspicuous coloration may be linked together, and how a species may derive benefit from one model in one area and from another elsewhere. *A. jodutta* is on the whole a forest species and therefore does not come into much contact with *Danaus chrysippus* L. But its very closely allied representative further south, *Acraea esebria* Hew., is intimately associated with *chrysippus* and occurs in a form with white subapical bar closely resembling that superabundant species. The general pattern in *chrysippus* and *schubotzi* is so similar that a species resembling one might well gain if it strayed into the locality affected by the other.

The *trophonius*-form of *Papilio dardanus* which in South Africa is associated with *chrysippus* and is far from uncommon, occurs only rarely in Uganda because the species here affects forests in which *chrysippus* does not occur. But it might well gain in Budongo from a certain degree of likeness to *Bematistes schubotzi*, and it would be most interesting to examine large numbers of *P. dardanus* females from this region. Mr. Jackson found no *trophonius* forms, but I have no record of the actual number of female *dardanus* secured by him. (See, below, the account of a specimen of f. *carpenteri*.)

#### Combination VI.

This centres round a form of *Bematistes epaea* (L.) transitional between the western *e. epaea* and the eastern *e. paragea* Gr. Sm. The males resemble the females but the pale areas are cream-coloured or yellowish, or even in some females almost white and in shape and size more like those of *e. epaea* than of *e. paragea*. The specimens are not uniform in appearance.

Primary model.	Acraeine mimic.	Nymphaline mimic.	Papilionine mimic.
<i>Bematistes epaea</i> , transitional ♂, ♀.	<i>A. lycoa bukoba</i> Eltr. ♂.	<i>Pseudacraea eurytus</i> f. near <i>obscura</i> Neave, ♂, ♀.	<i>Papilio cynorta</i> F. ♀ f. near <i>peculiaris</i> Neave.
34	12	7	3

The model and mimics are variable, but the correspondence between certain specimens is amazingly good (1935, *Proc. R. ent. Soc. Lond.*, 10 : 58, pl. 2). *Acraea lycoa* is of special interest because it is the males which fall into this combination, while the white-spotted females, of which 12 were taken, are more like a small *Amauris* (DANAINAE). The non-mimetic male of *Papilio cynorta* was not collected, but Mr. Jackson estimated it as "moderately common."

Finally, among the captures from Budongo must be mentioned the brown western form of female of *Acraea alciope*. Mr. Jackson recorded 17, of which he sent me 11. These are of the form *macarina* Btlr. in 2 cases, the rest tending towards *aurivillii*, to which the series forms a complete transition.

The forms of *Acraea althoffi* include also the ♂-like female form *drucei* Eltr., of which Mr. Jackson recorded 11; another specimen is a transition between *ochreate* and *drucei*, having some of the red of the latter; 3 of these were taken.

Mr. Jackson endeavoured to estimate the relative abundance in the field of the various forms, using ++ for very common, + for moderately common, — for rare, — — for very rare. The following represents his estimate. *Papilio dardanus* ♂, ++; ♀-f. *hippocoon*, ++; ♀-f. *planemoides*, —; *Papilio cynorta*, +;

*Pseudacraea eurytus* forms. +; *Bematistes schubotzi*. + +; *B. epaea* forms. + +; *B. macarista*, +; *B. macaria*, — —; *B. alcinoë*, — —; *B. tellus*, — —; *Acraea alciope*, + +; *A. jodutta*, + +; *A. lycoa*, + +; *A. althoffi*, + +.

The collection made by Mr. Jackson is in strong contrast to one made by Dr. S. A. Neave in the same Budongo forest from 11 to 15 December, 1911, which is now for the first time tabled here. The collection is incorporated in the national collection at the British Museum (Natural History), and I am indebted to the Keeper of Entomology for permission to study it and to publish these figures.

#### COMBINATION I.

*B. macarista* ♂ 9, *B. poggei* ♂ 0, ♀ 0, *B. macaria* ♂ 0, *A. alciope aurivillii* ♀ 3, ♂ 3, *Ps. eurytus hobleyi* ♂ 1, *poggeoides* ♀ 2, *E. phegea rattrayi* ♂ ♀ 0.

#### COMBINATION II.

*B. macarista* ♀ 7, *B. alcinoë camerunica* ♀ 0, ♂ 0, *B. macaria hemileuca* ♀ 0, *A. jodutta jodutta* ♀ 1, *A. althoffi althoffi* ♀ 0, ♂ 7, *Ps. eurytus tirikensis* ♀ 6, *Elymnioptis phegea bammakoo* 2.

#### COMBINATION III.

*A. jodutta* ♂ 5, *A. althoffi ochracea* ♀ 0.

#### COMBINATION IV.

*B. tellus* ♂ 3, *A. jodutta dorotheae* ♀ 0, *A. althoffi telloides* ♀ 0, *Ps. eurytus terra* ♂ 0. It may be recorded here that there is in the national collection a specimen of the female form of *P. dardanus* which approximates to the form *niobe* Auriv. which comes into this association. This is named as form *carpenteri* Poult. in the national collection, but the difference from *niobe* is one of degree rather than kind. This specimen was captured by the Rev. H. W. Tagart in the Budongo forest a good many years ago, and came to the British Museum with the Bethune Baker collection. It is interesting in connection with what was said previously about *dardanus* under Combination V.

#### COMBINATION V.

The only member of this association taken by Neave was a single ♀ of *B. schubotzi*.

#### COMBINATION VI.

*B. epaea* ♂ 4, ♀ 3, *A. lycoa media* ♂ 0, *Ps. eurytus* f. transit. 1, *P. cyrta transit. to peculiaris* ♀ 6, ♂ 5.

Neave also obtained 2 specimens of the western brown form of female *A. alciope*.

The two collections from the Budongo forest were made in different years, but at almost the same time of the year: Neave's in December, 1911; Jackson's in September, 1934. Probably both were from the same part of the forest, the vicinity of the government sawmills, from which open roads provide collecting grounds in an otherwise untouched forest. They differ in some remarkable items.

The main point of this paper is concerned with *Bematistes schubotzi*, of which Neave only secured a single female, which, until the Joicey collection was recently incorporated, remained the only example in the national collection. The Joicey specimens came from further west and south; the western rift valley in the Kivu region.

Jackson, however, found *schubotzi* "very common" in the Budongo forest, presumably it has multiplied considerably since Neave's visit. The association centred around it formed no less than 10.6% of Jackson's total captures of the

various associations. It seems to have partially replaced *Bematistes tellus*, generally so common in Uganda, whereas at Entebbe (on the north shore of Lake Victoria) the *tellus* combination is one of the best represented (Tables 1 and 2).

Thirdly, combination VI, centred round *Bematistes epaea paragea* is very much more abundant in the forest than at Entebbe.

Comparison of the Budongo fauna with that of Entebbe is of interest. Through the generosity of Dr. C. A. Wiggins, C.M.G., the Oxford University Museum received very large collections made at Entebbe without selection over prolonged periods: part of this was described by Sir Edward Poulton in 1911, 1<sup>er</sup> Congr. int. Ent. Bruxelles, 1910, 2: 504-506.

The collections made in 1909 (May 23-Oct. 17) and 1910 (April 8-Dec. 10) are here summarised, and it will be seen how the proportions of the several associations differ in the two localities: that centred round *B. schubotzi* (No. V) being unknown at Entebbe. It may be said here that Dr. Karl Jordan has informed me that the form of *Pseudacraea eurytus* belonging to this group (*schubotzoides* Carpstr.) is not represented in the Tring Museum; there are none in the national collection.

Collected at Entebbe by C. A. Wiggins in 1909 and (in brackets) 1910.

#### Combination I.

*A. Bematistes macarista* ♂, 85 (280); *B. macaria hemileuca* ♂, 0 (1); *Acraea alciope aurivillii* ♀, 52 (208); *Pseudacraea eurytus hobleiyi* ♂, 37 (46).

*B. B. poggei* ♂♀, 14 (96); *Ps. eurytus poggeoides* ♀, 1 (1); *Ps. küdnowi hypoxantha* ♂♀, 2 (8); *Elymnias phegea ratrayi* ♂♀ 0 (2); *Papilio dardanus planemoides* ♀, 6 (13).

#### Combination II.

*B. macarista* ♀, 39 (175); *B. alcinoë camerunica* ♀, 11 (36); *B. macaria hemileuca* ♀, 0 (0); *A. jodutta jodutta* and *carmentis* D. and H., ♀, 48 (64); *A. althoffi althoffi* ♀, 3 (14); *Ps. eurytus tirikensis* ♀, 33 (85); *E. phegea bammakoo* ♂♀, 1 (8).

#### Combination III.

*A. jodutta* ♂, 75 (70); *A. althoffi ochreatea* ♀, 8 (17). N.B.—Unfortunately the writer did not separate this form from *telloides*, which is probably included with it.

#### Combination IV.

*B. tellus eumelis* ♂♀, 92 (514); *A. jodutta dorotheae* ♀, 25 (50); *A. althoffi telloides* ♀, 8 (17), but see previous note; *Ps. eurytus terra* ♂♀, 18 (43); *P. dardanus niobe* ♀, 2 (6).

#### Combination V.

Not represented.

#### Combination VI.

*B. epaea paragea* ♂♀, 16 (37); *A. lycoa* (not counted); *Ps. eurytus obscura* ♂♀, 0 (2); *P. cynorta peculiaris* ♀, 1 (3).

The following Table, No. 1, expresses the above absolute numbers for both localities in percentages, showing the proportion of each combination in the total captures. The heading "Acraeas" refers to the percentage number for each combination of the smaller Acraeines which are usually counted as models of less importance than the more conspicuous Planemas.



TABLE 1.

Group.		Entebbe, 1909.	Entebbe, 1910.	Budongo (Neave).	Budongo (Jackson).
I.	%age of Total  %age of Acraeas	40.5  26.4	32.8  31.7	26.7	26  83.2
II.	„  „	23.5  38.1	22.8  20.1	33.3	24.7  67.
IV.	„  „	31.3  22.7	41.3  10.6	6.7	14.9  74.3
V.	„  „	0.  0.	0.  0.	2.2	10.6  16.
VI.	„  „	4.7  0.	3.  0.	31.1	23.8  33.9

The strength of the Acraeas varies greatly, and in order to obtain an insight into the relations of the major members of the associations they have been left out of account in Table 2. They seemed extremely scarce when Dr. Neave collected in Budongo, but no selection was made in favour of the larger species, so that the small number of Acraeas cannot thus be explained.

TABLE 2.

Group.	Entebbe, 1909.	Entebbe, 1910.	Neave.	Jackson.	
I.	35.4	32.8	26.7	10.7	The figures give the percentage of each combination, in the total captures of all combinations, for each locality, the smaller Acraeines being disregarded.
II.	33.	22.8	33.3	18.4	
IV.	27.3	41.3	6.7	7.7	
V.	0	0	2.2	20.4	
VI.	4.1	3.	31.1	42.7	

Table 2 shows that at Entebbe the two years agree very well, and that as regards Budongo both collections agree in the diminution of combination IV and the increase of combination VI. Jackson's collection shows nearly ten times the number of combination V present in Neave's collection, while there are none from Entebbe.

The increase in V and VI in Jackson's collection over Neave's causes a drop in the proportionate number of I and II.

The following is a summary :

1. A species of *Bematistes* formerly extremely rare has become abundant in the Budongo forest, western Uganda, and has associated with it forms of *Acraea althoffi* Dew. and *Pseudacraea eurytus* (L.) hitherto unknown.

2. The species of *Bematistes* serving as models for *Ps. eurytus* exist in the Budongo forest in relative proportions quite different from those at Entebbe, in central Uganda, and their proportions are reflected in the associated mimics.

3. These results confirm previous work on these species from other parts of Uganda and refute explanations of mimicry which depend upon chance and consanguinity such as that urged by Heikertinger.

# ON AN ABNORMALITY OF THE EIGHTH ABDOMINAL SEGMENT IN FEMALES OF *LOCUSTA MIGRATORIA* L. (ORTHOPTERA)

By A. G. HAMILTON, B.Sc., Ph.D., F.R.E.S., and W. M. MILNTHORPE, B.Sc.

## INTRODUCTION.

IN the course of work conducted in the locust laboratory of the Imperial Institute of Entomology, three females possessing abnormalities of the eighth abdominal segment were discovered. These constituted the only cases of abnormality observed among the several thousand insects which have been handled over a period of three years.

Two of the specimens A and B, were from the same  $F_9$  generation. The parent stock was of the phase *gregaria* and from east Africa (ssp. *migratorioides* R. & F.). Specimen C, however, belonged to an  $F_5$  generation, the parent stock being of the phase *solitaria* and from Algiers, north Africa (probably ssp. *migratoria* L.; see Uvarov and Hamilton, 1936).

All were bred in the laboratory under optimum conditions (90° F. and 65% relative humidity).

Specimens A and B were among the progeny produced by a hatching from two egg-pods which had been kept in the same cage and of the 44 hoppers which hatched, 35 became adult and of these 13 were females. With the exception of A and B, all these were found to be quite normal.

Specimen C was the only abnormal individual from among 76 locusts which hatched from two egg-pods kept in the same cage.

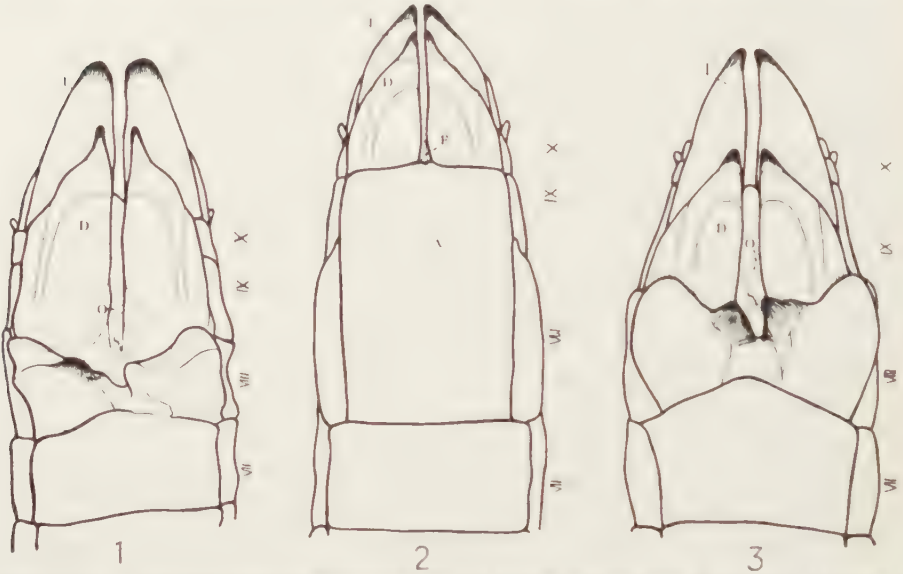
These three cases of abnormality are believed to be the first of the kind recorded for ACRIDIDAE.

## *General description and comparison with the normal female and the developing hopper.*

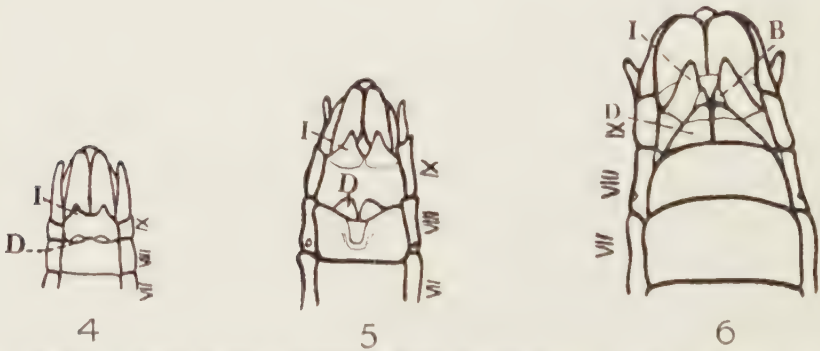
Fig. 1 represents a semidiagrammatic ventral view of abdominal segments seven to twelve of specimen A. On comparing this with fig. 2 which represents the corresponding segments of a normal individual, it may be seen that the subgenital plate has failed to develop as a prolongation backward from the eighth sternite, so that the anterior and posterior valves of the ovipositor are almost completely exposed. Instead, the eighth sternite has an uneven posterior margin and shows signs of folding, while the left half bears a distinct conical projection which is strongly chitinised and has hairs similar to those commonly present on the valves of the ovipositor. Other differences are that the normal folding between the seventh and eighth segments is drawn back and incomplete. The openings of the vagina and spermatheca are apart, whereas normally they lie side by side, and correlated with the absence of the subgenital plate there is no egg guide. Further, the anterior pair of ovipositor valves are shortened and do not project so far back as in an average individual. The interior and posterior valves are normal.

Specimen B is not figured since it resembled A in every particular, except that in this case the conical projection borne by the eighth sternite is on the right side, and the folding between the seventh and eighth sternites is drawn back, but complete.

In specimen C (fig. 3) the abnormality has been carried a stage further. In this case the sternite of the eighth segment bears a pair of almost similar



FIGS. 1-3.—1. Ventral view of segments seven to twelve of specimen A showing abnormal eighth sternite with the conical projection developed on the left side ( $\times 9$ ); 2. Ventral view of segments seven to twelve of normal female ( $\times 9$ ); 3. Ventral view of segments seven to twelve of specimen C showing the abnormal eighth sternite with the conical projections developed on both sides ( $\times 9$ ).



FIGS. 4-6.—4. Ventral view of segments seven to twelve of a normal 1st-instar female hopper ( $\times 15$ ); 5. Ventral view of segments seven to twelve of a normal 2nd-instar female hopper ( $\times 15$ ); 6. Ventral view of segments seven to twelve of a normal 3rd-instar female hopper ( $\times 15$ ).

#### ABBREVIATIONS USED IN THE FIGURES.

I = posterior valve of ovipositor; D = anterior valve of ovipositor; E = egg guide; A = subgenital plate; B = interior valve of ovipositor; O = external opening of vagina; S = external opening of spermatheca; VII to X = Abdominal segments seven to ten.



conical projections which are highly chitinated and bear hairs. As in specimen B, the folding between the seventh and eighth segment is complete and drawn back. In all other respects the abnormalities shown are identical with those already mentioned for specimens A and B.

Specimen A died 24 hours after becoming adult, but B lived for 15 days. An attempt was made to breed from B, but proved unsuccessful. The locust was kept in a cage with a male of the same  $F_9$  generation, but no pairing occurred although it was attempted by the male. A batch of eggs was laid on the sandy floor of the cage, and although they were subsequently collected and buried in moist sand, they failed to develop.

Specimen C lived a normal life period of three months. Pairing with a male of the same  $F_5$  generation was effected, but it is not known whether fertilisation occurred. Five egg-pods were laid, two slightly buried in the sand and the others on top; all failed to hatch. It is probable that the shortened anterior pair of ovipositor valves prevented effective burrowing by the abdomen.

In each case a dissection of the internal reproductive organs was made and they were found to be quite normal with regard to their size and shape, number and position.

It appeared that in each case the eighth segment was attempting to produce an additional pair of ovipositor valves, and the absence of the subgenital plate, the separation of the openings of the vagina and spermatheca and the other abnormalities were correlated with this and had no other significance. Hopper stages were therefore examined in order to see what light the origin and development of the ovipositor valves in a normal individual would throw on the homology of these abnormal conical processes. In a 24-hour-old 1st-instar hopper, the posterior pair of valves appear as a pair of minute conical outgrowths which arise from the margin of the ninth sternite and can be clearly seen (fig. 4 I). The anterior pair of valves are also present as small flattened lobes produced from behind the margin of the eighth sternite and at this stage still lie in the membrane behind the eighth segment (fig. 4 D). By the 2nd instar the posterior pair of outgrowths have considerably increased in size (fig. 5), while the anterior pair of flattened lobes have increased in size pushing out the covering membrane with them, and appearing as a pair of distinct conical outgrowths. The mid-posterior margin of the eighth sternite, as a result of the position of the growing pair of anterior valves, is prevented from growing back with the elongating eighth segment. By the 3rd instar (fig. 6) both the posterior and anterior pair of valves have further increased in size and the posterior margin of the eighth sternite has grown back and is almost complete. The interior pair of valves also appears at this stage as minute outgrowths from the anterior bases of the posterior pair.

#### DISCUSSION.

Reference to the work of Crampton (1917), Walker (1919), Chopard (1920), Nel (1929) and Snodgrass (1935) shows that they are in agreement concerning the segments on which ovipositor valves develop in so far that the ninth segment gives rise to the posterior, and subsequently the interior pair of valves, and that the eighth segment produces the anterior pair. Also all are agreed that the posterior pair arises from the sternite of the ninth segment and the interior pair from the anterior bases of the posterior pair. With regard to the position of origin of the anterior pair of valves on the eighth segment, Chopard (1920) and Nel (1929) state that they arise from the posterior margin

of the eighth sternite in a similar way to the posterior pair from the ninth. Snodgrass (1935), on the contrary, states that they arise from behind the margin of the sternite of the eighth segment.

We found that in the 1st-instar hopper, the anterior pair of valves arose as a pair of flattened lobes from behind the margin of the eighth sternite. Now, in the case of the abnormal conical processes produced by the eighth sternite, it may clearly be seen that in each of the cases they were produced from the posterior margin of the eighth sternite (figs. 1 and 3). This means that they are analogous to the posterior pair of valves which are normally produced by the ninth segment. Comparing specimen C (fig. 3) with a normal 1st-instar hopper (fig. 4) it may clearly be seen that there is a close resemblance between the developing pair of posterior valves (I) and the abnormal conical processes borne by the eighth sternite of specimen C.

In each of the three cases, the ninth segment has produced a normal posterior and interior pair of ovipositor valves, while the eighth segment has produced the normal anterior pair which arise from behind the distal margin of the eighth sternite and has attempted to produce an additional pair which arise from the distal margin and are analogous with the posterior pair of valves, such as are normally produced by the ninth segment. In fact, this is a case of supernumerary structure arising from a segment preceding that by which such a structure is produced normally. Moreover, the supernumerary valves are produced heterochronically since their structure in the adult stage is similar to that observed normally in the 1st-instar hopper. Since the heterochronic appearance of supernumerary ovipositor valves has been observed on three different occasions and appeared in two separate stocks, the phenomenon cannot be due to accidental causes and is of considerable interest from the point of view of organogenesis.

Although normally the function of the eighth and ninth segments is separate and specialised with regard to the types of ovipositor valve they produce, it would appear from these three cases of abnormality that on occasion the eighth segment can assume the function of the ninth in producing a type of valve similar to that produced by the ninth.

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